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THE VASCULAR ANATOMY OF PIPER METHYSTICUM
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 218

RACHEL E. HOFFSTADT

(WITH TWENTY-THREE FIGURES)

Historical

LINNAEUS placed the Piperaceae in the monocotyledons among the Aroidaceae; JUSSIEU held that they were near the Urticaceae; KUNTH (8) and BLUME ranked them with the monocotyledons. DE CANDOLLE (4), however, following JUSSIEU, stated that the embryo characters indicated their dicotyledonous character. ENGLER and PRANTL (5) put the tribe Piperales among the lower Archichlamydeae. Included in it are 4 families: Saururaceae, Piperaceae, Chloranthaceae, and Lacistemaceae. The genus *Piper* contains over 1,000 species. MIQUEL (10) separates 7 species from the original classification on the basis of the presence or absence of his so-called "stipula oppositifolia" and persistence of the petiole. Among these is *Piper methysticum* Forst., which he calls *Macropiper methysticum*. ENGLER and PRANTL (5), using as a basis of their classification of these two genera the method of branching in the floral regions, retain the name of FORSTER.

Piperaceae have attracted much attention because of their anomalies, both in anatomical and reproductive features. The former have been described in many species. MIQUEL (10) asserted that the internode of the stem ends blindly in the petiole, and the next internode develops from a bud between the petiole and the end of the foregoing node. He stated also that there are alternate, opposite, and whorled leaves on the same branch. The latter he concluded were atrophies, and the number of internodes which would have been produced would have been the same number as the whorls of leaves. SANIO (11) described in detail the structure and the course of the bundles in the stem of *Peperomia blanda*. SCHMITZ (12) verified the work of SANIO in *Peperomia*. He concluded that the peripheral bundles in *Piper* were joined at

their base with the inner bundles of the stem. The small bundles of the leaf trace come from branches of the peripheral bundles. They, as well as the central bundles, go with or without branching into the petiole, which is merely a continuation of the stem.

In an elaborate discussion of the vascular anatomy of the Piperaceae, WEISS (19) deals with 11 species of *Peperomia* and 8 of *Piper*, and draws the conclusion that in the Piperaceae there is a transition from the monocotyledonous to the dicotyledonous type of bundle.

By far the most detailed account is that of DE BRAY (3). He used 4 species of Saururaceae, 16 species of *Piper*, 3 species of *Artanthe*, and 11 species of *Peperomia*. In *Piper* he found 2-4 rings of bundles arranged in two systems, the peripheral and the pith systems. The peripheral bundles are of two sizes; the outer ring is completed by an interfascicular cambium; the leaf trace comes from a peripheral ring, which in the node below is a branch of the central bundles; the vascular supply of the axillary buds is from both peripheral and central bundles. He compares the families of the group, but shows no relationships.

In VAN TIEGHEM'S (17) work on the mucilage canals of *Piper* he describes in detail the stem of *Piper nigrum*. He found that there are two circles of bundles; that the pericycle becomes lignified late in the growth of the stem; that the cambium for a long time cuts off segments only on the side toward the pith, and may cut off very late a few segments on the other side; that the mucilage canals vary in location with different forms and are not continuous through the nodes; and that the canal of the petiole is not continuous with that of the branch.

The present study of *Piper methysticum* was taken up with the idea of giving a modern interpretation to the vascular structure, and to ascertain whether the stem keeps pace with the gametophyte of the group.

Material

I am indebted to Dr. W. J. G. LAND for the material for this study. It was collected on the Island of Tutuila, Samoa (fig. 1). The plant is a native of the South Sea Islands, and is commonly

called *Ava* or *Kava*, the natives extracting from its roots the national beverage bearing that name.

It becomes a shrub 1-1.5 m. in height and is propagated mostly by cuttings. No seedlings were obtainable. The leaves are ovate, 18-25 cm. in diameter, with a deep cordate base and a short acuminate apex. The blade is bright green, smooth above, and bears fine multicellular hairs on the veins beneath. It is distinctly petioled, the petiole having a sheathing base and



FIG. 1.—*Piper methysticum* growing in Samoa

a deciduous stipule. The leaves are alternate and the dense flower clusters are borne opposite them. The internodes are 7-10 cm. long, the nodes being swollen, smooth, and in the older ones irregularly spotted. Both old and young stems have an herbaceous appearance. The largest nodes examined were 2.75 cm. in diameter, and the smallest were 2 mm.

For the sake of comparison *Piper umbellatum* (*Heckeria umbellata* Kunth) was used, the material being obtained from plants brought from Mexico. In shape and size the leaves resemble those of *Piper methysticum*. The petiole has a sheathing base;

the nodes are swollen and marked with several distinct rows of spots; the internodes are 5-9 cm. long and when young are covered with dense rows of hairs, giving a ridged appearance; the older internodes are smooth but spotted.

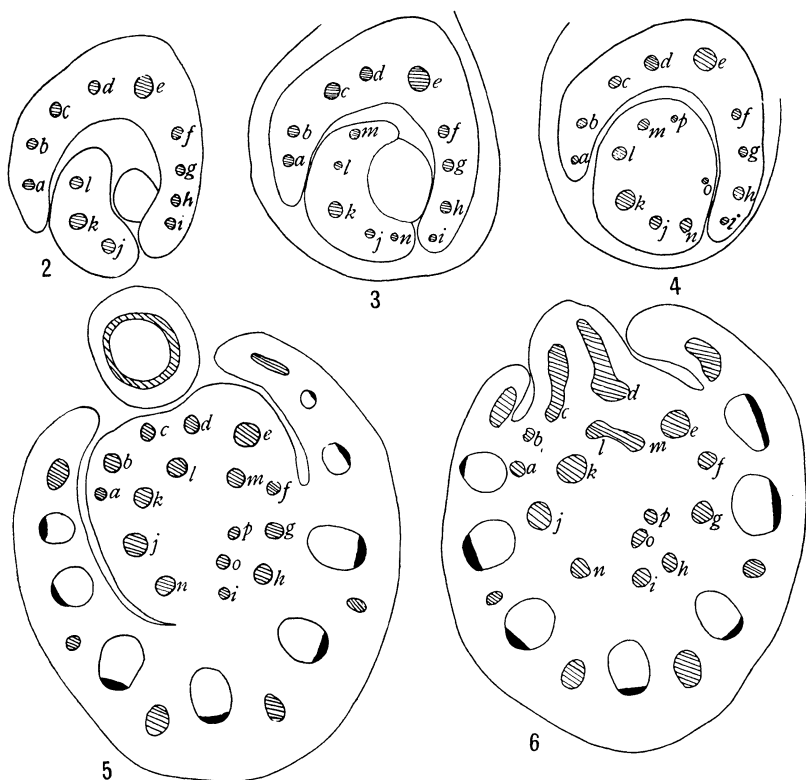
The younger stems and nodes were cut in paraffin at 25-30 μ and complete series obtained. The largest stems and nodes were treated with hydrofluoric acid for one week and then sectioned at 30-50 μ with a sliding microtome, in this case also the series being complete. The safranin Lichtgrün stain was used.

Origin and course of stem bundles

The stem of *Piper methysticum* contains at maturity three rings of bundles, one peripheral and two within the pith, the bundles being foliar. The terminal bud is enveloped in the sheathing base of the youngest leaf. In some cases a bud was found within the sheath of a single leaf with as many as 3 leaves, each of which was inclosed in the base of the petiole just beneath it.

The leaf primordium appears on the stem tip early and forms about it a semicircle, and 5-7 procambial strands are soon differentiated. These connect with the first strands of the stem (figs. 2-4, $j-p$). Strands $j-p$ are the strands of the youngest leaf (node 1); k is the first to be differentiated; j and l follow quickly; o and p come last. The bundles of the second leaf (node 2) are represented by the series $a-i$. At node 1 the stem contains a single row of scattered bundles. These bundles ($j-p$) become the inner bundles of the stem at node 2, and $a-i$ of leaf 2 become the peripheral bundles (fig. 5). Through the following internode these two sets of bundles run approximately parallel and become the inner rings of the next node (node 3, fig. 6). The union of the two inner rings takes place here. Five methods of joining were observed in the case of the undifferentiated strand: (1) two strands from the same ring may join (fig. 8, lm); (2) two strands from different rings (fig. 7, ak); (3) one strand may divide and join a strand of a different ring (fig. 7, g^1p); (4) two strands from the same or different rings may unite and then join a branch of a strand from either ring (fig. 9, efg , ino); (5) three strands may join, the result of this, for a short time, being a single inner ring (figs. 9, 10, dlm).

The peripheral bundles at any node may branch. In older nodes this branching may occur just before the peripheral bundles become pith bundles, and part remain in the peripheral ring; the latter will then connect with the bundles of the leaf at the node below (fig. 19).



FIGS. 2-6.—Transverse section through a terminal bud of *P. methysticum*, showing the course of the bundles; $\times 168$.

The coalescence of the branches of these bundles does not always occur at the node, but may occur above or below it, as follows: (1) branches of the same bundles may join before passing through a node; (2) branches from different bundles may unite; (3) branches of a peripheral bundle of the internode above may join a peripheral bundle of the internode below. Not infrequently strands isolated in the anastomosing of the pith bundles at any

node may join the peripheral bundles at that node. The peripheral bundles of any internode, therefore, when young will consist of one set of foliar bundles only; and when older may contain portions of the foliar bundles of the leaves of 3 nodes.

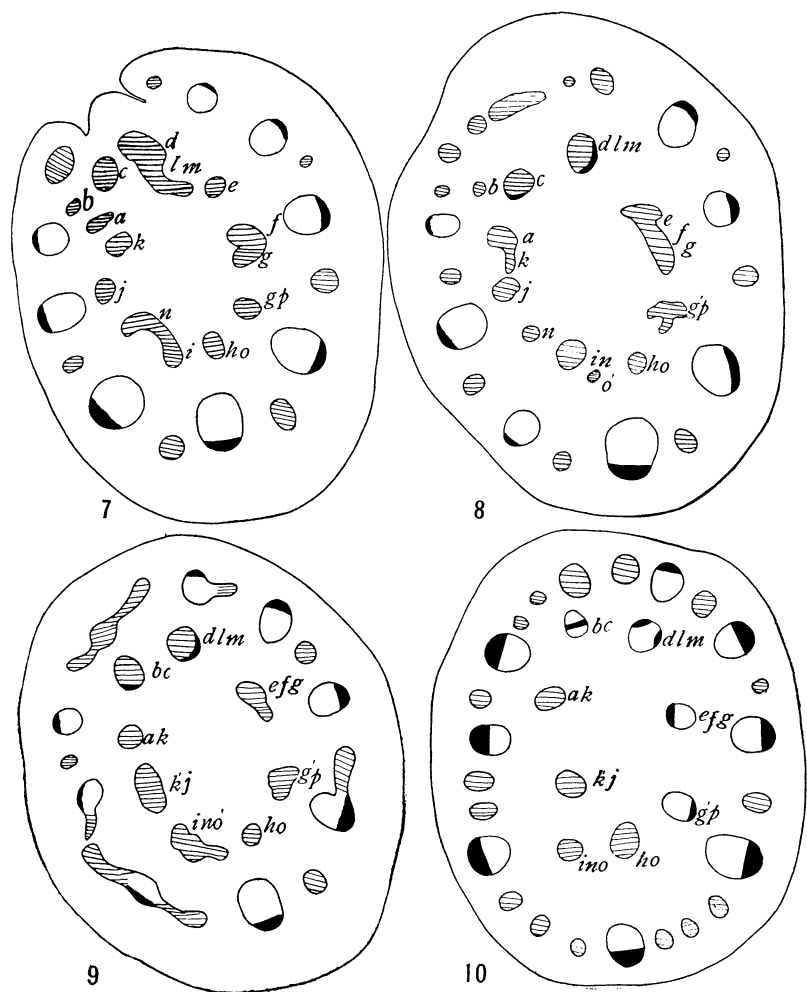


FIG. 7-10.—Transverse sections through a terminal bud of *P. methysticum* showing course of bundles; sections follow those of figs. 2-6; $\times 168$.

The node in which the strands have become differentiated presents a most complicated appearance. One often finds for

a short time xylem entirely surrounding phloem, and vice versa. Bundles may join with either the phloem or xylem together. They may lie side by side and union may occur either in the xylem or in the phloem. Not infrequently the xylem of two bundles may unite, and the phloem of a third join the phloem of either of the others. Strands become separated from bundles and several of these may coalesce to make a bundle, or they may join with other bundles. One often gets cross-sections and longitudinal sections of the same bundle in the same section.

The bundles in one internode are in the periphery, and through the following two internodes are pith bundles. The position in the pith often gives the appearance of two complete rings and one-half of a third ring, when the number of bundles is large; but careful study shows that there are really only two rings. The number of bundles reaches 45-50 in the pith.

Description of stem in detail

As previously stated, the stem of *Piper methysticum* has two sets of bundles which may be designated as the peripheral ring and pith or medullary rings, two in number, and an irregular half-ring which gives the appearance of a third ring at times. The bundle type is open collateral endarch, oriented for the most part in the usual manner. Sometimes, however, one finds the protoxylem points appearing in reverse orientation (fig. 10, *e-g*). Union is often incomplete and one finds double bundles persisting in the internode, and these may be of two types. The xylem points or the phloem points may be together (figs. 11, 12).

The peripheral ring of bundles is formed of two sizes: the primary, those differentiated first; and the secondary, termed supplementary by DE BRAY (3) (fig. 13). The secondary bundles are branches of the primary bundles and lie between them. More than one primary bundle may contribute to a secondary one (fig. 9); that is, two bundles may branch and the branches join. The number of secondary bundles varies from none to 3, according to the age and size of the stem. Near the tip there are none (fig. 4), as observed by SCHMITZ (12).

The inner rings of bundles are approximately the same size. This does not differ from the majority of the species of *Piper*.

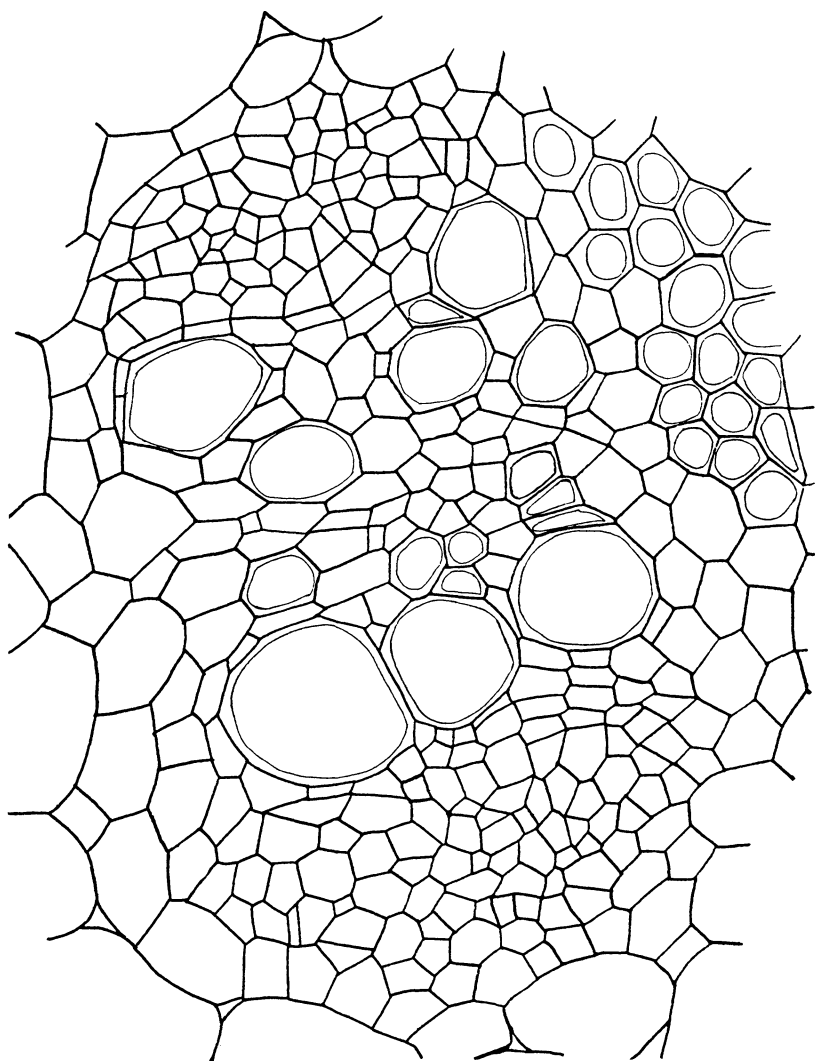


FIG. 11.—Detail of a double bundle with phloem on the outside and lignified tissue at the side; $\times 820$.

Between the pith and the peripheral ring of bundles in the young stem is a continuous band of parenchyma, 4–6 rows thick, which

early becomes lignified (figs. 13, 14). Later, owing to growth of the bundles, this band is broken and patches appear only at the inner portions of the bundles (fig. 18).

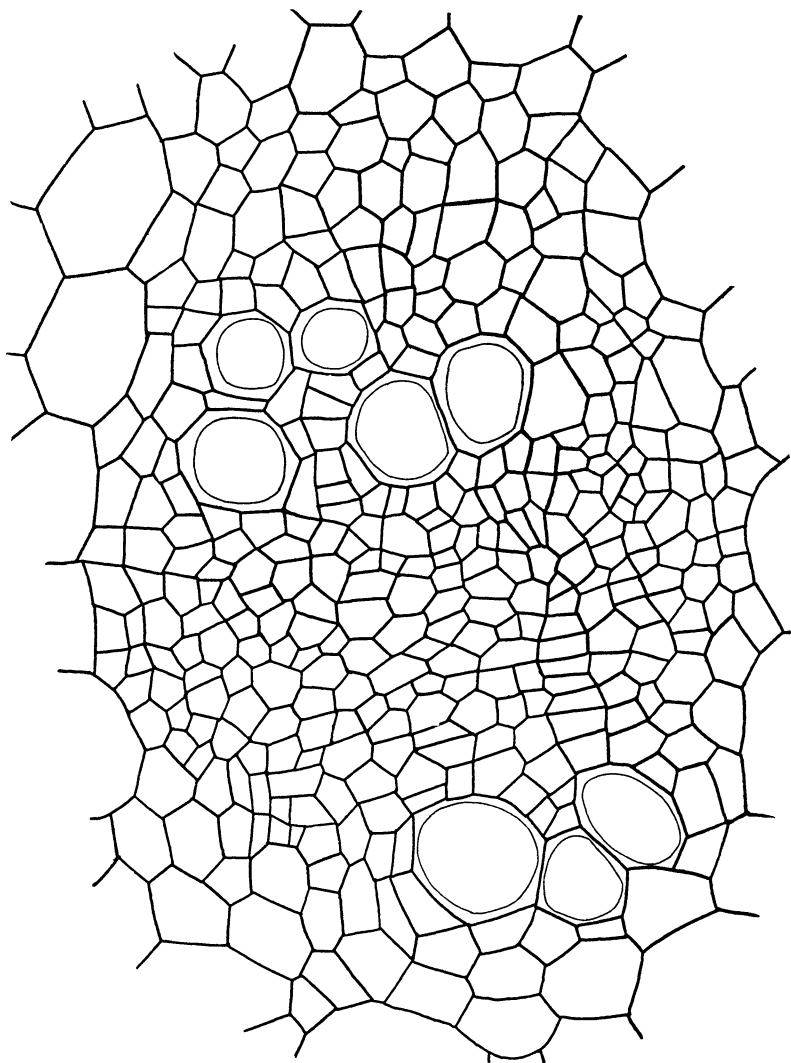
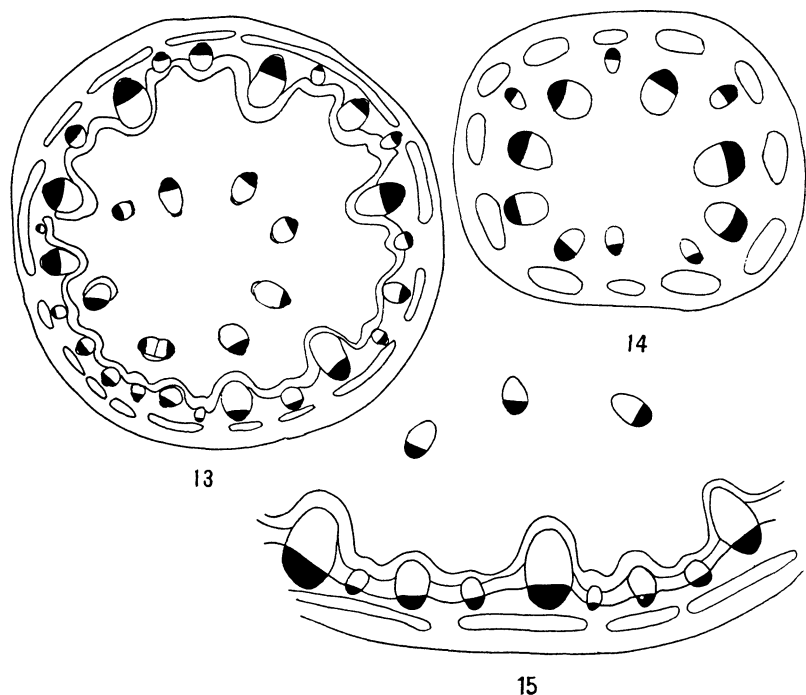


FIG. 12.—Detail of double bundle with xylem points outside; $\times 820$

The pericycle consists of only a few cells (fig. 16) just outside the bundles in both the peripheral and pith systems, and nowhere else. It can be distinguished easily in the young stems by the

dense cell contents. Late in the history of the plant the pericycle becomes lignified. There is no differentiated endodermis in either old or young stems.

In the cortex of the young stem is a continuous band of tissue 7-8 cells wide, which responds to the test for suberin (TUNMANN 16). This is in patches in the older stems. The intercellular spaces of the pith are very large.



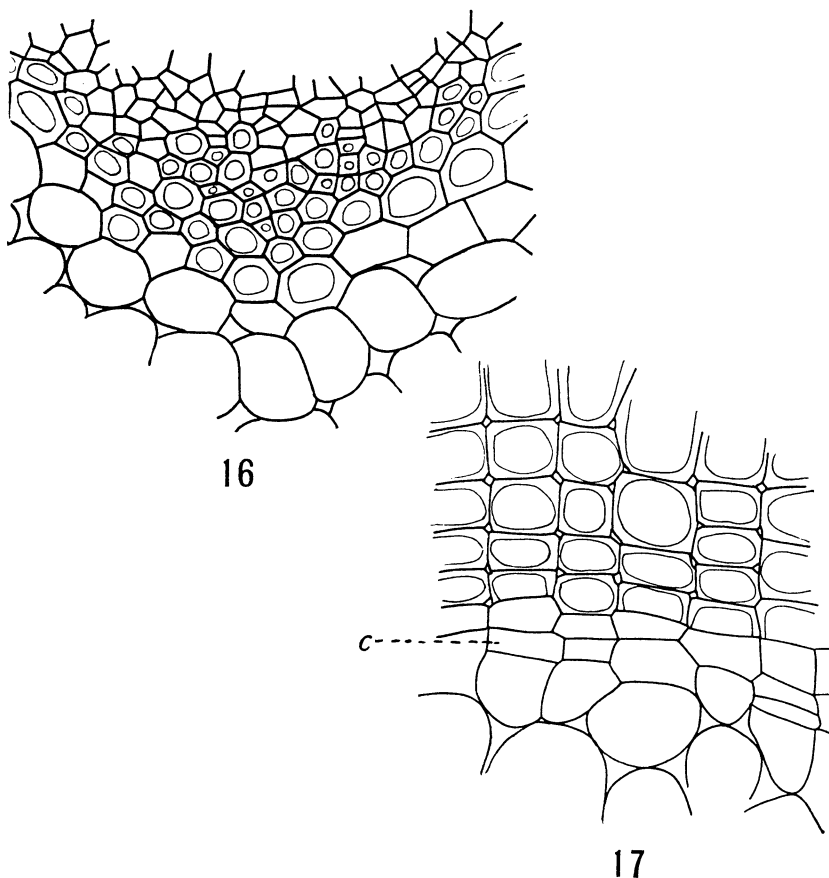
FIGS. 13-15.—Fig. 13, young stem of *P. methysticum* after differentiation has been completed, $\times 80$; fig. 14, petiole, $\times 101$; fig. 15, sector of stem after inter fascicular cambium has been developed, $\times 101$.

Secondary activity in the stem

There are two methods by which the stem of *Piper methysticum* enlarges: (1) by active division of pith cells; (2) by cambial activity.

1. In the center of and at irregular intervals throughout the pith, groups of cells will divide actively throughout the internode.

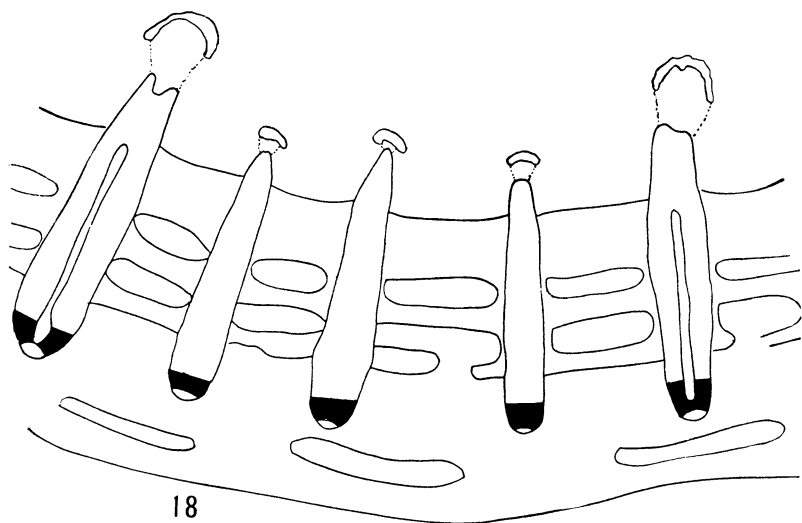
2. Each bundle of both the peripheral and pith rings has a cambium. The inner ones do not enlarge greatly. The outer or peripheral bundles lay down a ring of wood often 4-5 mm. in thickness. The proportion of xylem to phloem is about 8:1 (fig. 18).



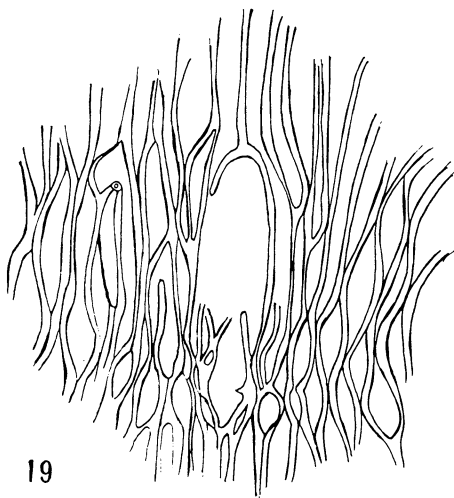
FIGS. 16, 17.—Fig. 16, detail of pericycle of *P. methysticum*; fig. 17, detail of medullary ray; C, cambium; $\times 820$.

Late in the history of the stem an interfascicular cambium appears (fig. 15), which cuts off segments on the inside only; very late a few segments may be cut off on the other side (fig. 17). This closes the stem cylinder. The interfascicular cambium appears much later in the nodes and remains active much longer.

VAN TIEGHEM calls attention to the one-sided action of the cambium in his work on *Piper nigrum*.



18



19

FIGS. 18, 19.—Fig. 18, section of peripheral ring of the bundles of *P. methysticum* at a mature node, showing banded appearance of the rays, $\times 35$; fig. 19, tangential section of peripheral bundles, showing branch gap; $\times 7$.

The medullary ray becomes lignified and in longitudinal section shows pitted cells. At the node in the largest stems avail-

able, cells next to the cambium do not lignify and remain active. These are also scattered at irregular intervals throughout the ray. In section this gives the ray an irregular banded appearance (fig. 18). There are no growth rings. Much of the wood parenchyma touching the pith retains its activity at the node and divides long after secondary wood has been laid down. This pushes the primary vessels of the bundles apart at great distances, as well as the cells of mechanical tissue (fig. 18).

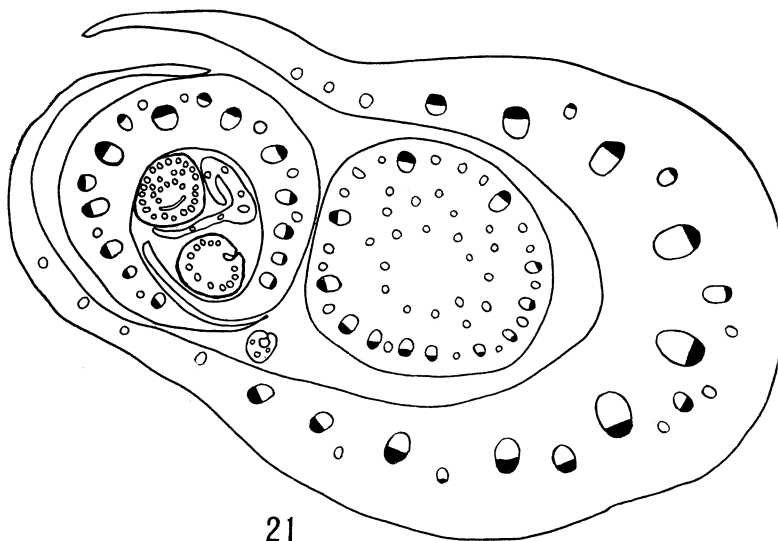
The stem when young is packed with starch and piperin. Mucilage cells are scattered throughout it, and the buds especially are covered with mucilage.

Leaves

The leaves have distinct petioles, the sheathing bases of which extend entirely around the stem, which becomes narrow opposite the point of insertion of the leaf. The leaf traces vary in number from 7 to 14. The bundles may be of two sizes. The lower part of the petiole is flattened on one side; the upper part is circular. The bundles form a crescent in the lower portion of the petiole (fig. 21), this crescent being made complete in the upper portion by the branching of the bundles at the points of the crescent (fig. 14). The secondary bundles form a more or less complete outer ring, are of the same type as those of the stem, and anastomose at any portion of the petiole. Union of the primary and secondary bundles, however, takes place before the traces enter the blade, which has 7-9 strong palmate veins, the 3 median ones running parallel for a while before they swing out laterally. The vernation of the leaf is involute.

Branching

Buds are borne in the bases of the sheathing petiole, the number varying from 1 to 3. The appearance of a single bud is often to one side instead of in the median position, which probably accounts for the appearance of branches coming from the side of the leaf. The buds are invested by a large amount of mucilage. The central bundles of the branch connect with those of the stem, and the peripheral ones connect with the peripheral bundles of the



FIGS. 20, 21.—Fig. 20, transverse section of mature and young buds, $\times 32$; fig. 21, transverse section through the base of a petiole, showing branches arising in axils of abortive leaves, $\times 28$.

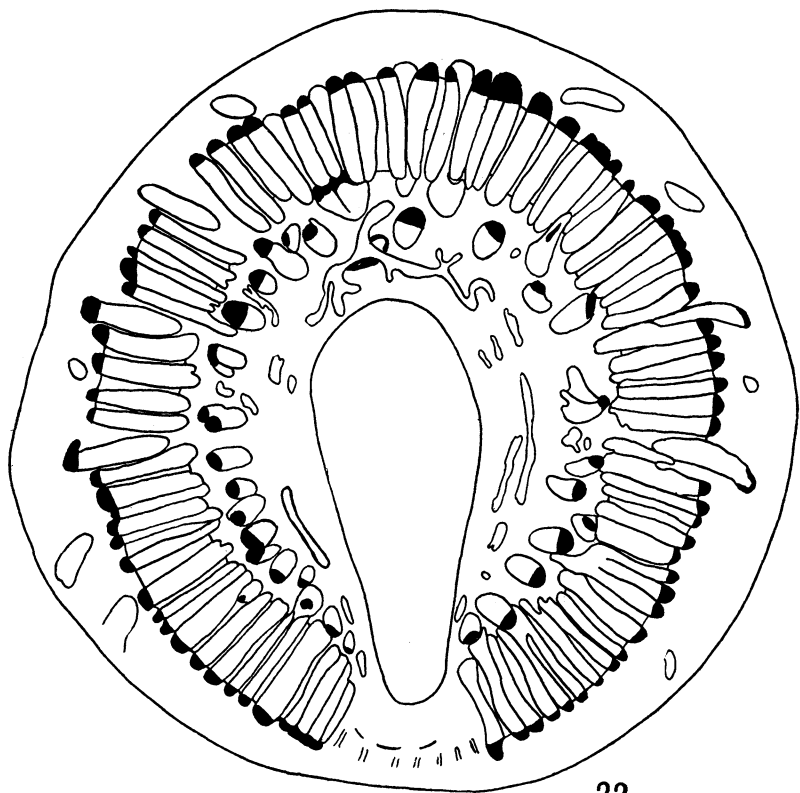
stem (fig. 20). In two cases it was observed that the branch did not develop in the axil of a leaf where only the blade was developed (fig. 21), which was due probably to the pressure caused by the enveloping sheaths of the preceding leaves.

Piper umbellatum

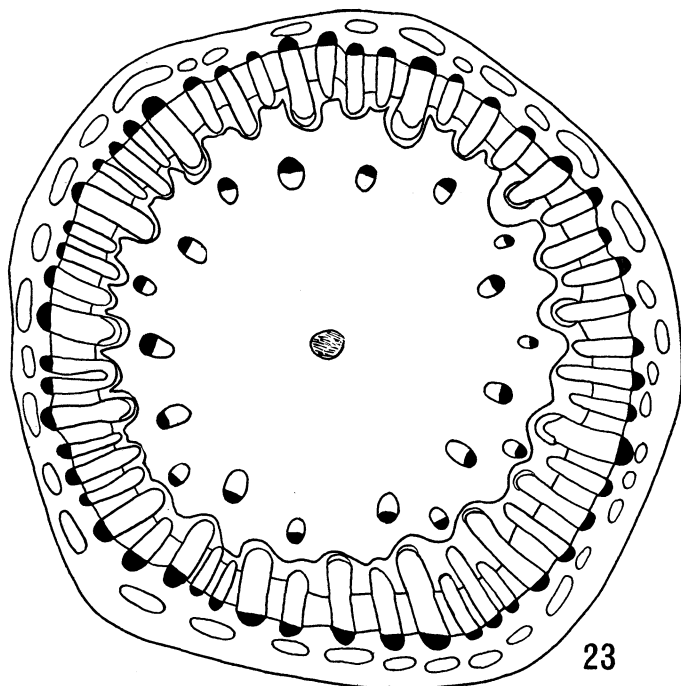
The stem of *Piper umbellatum* is not essentially different from that of *Piper methysticum*. At maturity it has only one ring of pith bundles. The bundles, instead of traversing two nodes as internal bundles before fusing with the next group, traverse but one (fig. 22). The young plants are covered with hairs, both unicellular and multicellular. The number of leaf traces is 7-9. In the young stem there is an abundance of mucilage scattered in all regions. In the old stem a single mucilage canal appears in the center, which is continuous through the nodes and in the branches; VAN TIEGHEM found none that was continuous through the nodes (fig. 23).

Summary

1. The stem of *Piper methysticum* consists of two systems of bundles, peripheral and pith, the latter being in two rows.
2. The peripheral bundles are of two sizes: primary, the larger; secondary, the smaller. The latter are branches of the former.
3. The bundle type is collateral endarch.
4. The bundles are of foliar origin.
5. The bundles, after entering the stem, remain in the peripheral region through one internode and then traverse the pith for two internodes.
6. Both the peripheral and pith bundles show anastomoses.
7. The pericycle consists of only a few cells outside the bundles, which become lignified.
8. There is no differentiated endodermis.
9. The stem enlarges by cambial activity and divisions in the pith region.
10. An interfascicular cambium appears late in the internode and cuts off segments only on one side; it comes still later in the nodes.



22



23

FIGS. 22, 23.—*P. umbellatum*: fig. 22, section through mature node; fig. 23, section through internode; $\times 12$.

11. Leaf traces are many.
12. The base of the leaf is sheathing and vernation is involute.
13. Buds vary in number and position.
14. *Piper umbellatum* differs from *Piper methysticum* in the following ways: (1) one ring of pith bundles only; (2) the mucilage canal runs through the center of stem and node; (3) the bundles run through one internode only in the periphery and one in the pith before fusing with those of the leaf above.
15. Both stems are packed, especially when young, with starch, piperin, and mucilage.
16. There are no growth rings.

Discussion and conclusions

The anatomy of *Piper methysticum* and of *Piper umbellatum* agree for the most part with the anatomy of the species of *Piper* already described; especially is this true in reference to the work of DE BRAY (3; see also DE BARY 2). VAN TIEGHEM reports a differentiated endodermis in all species of *Piper*, but this was lacking in these forms.

The question of most importance is the relationship shown by these forms. SINNOTT and BAILEY (13, 14) assert that the most primitive condition of angiosperms was woody, and that there is a tendency toward the herbaceous habit in the more recent groups. These forms show a tendency toward elimination of secondary growth and a breaking up of the woody cylinder in the following characters: (1) the pericycle is broken and all that remains is a small patch outside of each bundle; (2) the interfascicular cambium appears late in the internode and still later in the nodes; when it does occur the activity is primarily on one side; (3) there is a tendency toward the scattering of the bundles in the pith. These, together with the sheathing base of the petiole, the multi-lacunar (SINNOTT 13) type of node, and the anastomosing of the bundles at the side, show a monocotyledonous tendency. Moreover, the embryo sac of the group shows the elimination of one division in oogenesis.

One may conclude from this combination of characteristics that *Piper methysticum* and *Piper umbellatum* lie in a group well

toward the level of monocotyledons, and the conclusion is borne out by the female gametophyte.

The writer is indebted to Professor JOHN M. COULTER for suggestions and criticisms, and to Dr. W. J. G. LAND for the material used and for direction and encouragement during the investigation.

UNIVERSITY OF CHICAGO

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